

DO MIGRANT SWAINSON'S HAWKS FAST *En Route* TO ARGENTINA?

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ABSTRACT.—Some observers assert that Swainson's Hawks (*Buteo swainsoni*) do not feed during their migration between North America and Argentina, which lasts 5 or more weeks. Evidence for such a prolonged fast is anecdotal, speculative, and equivocal. A migratory fast of this duration is physiologically and ecologically improbable. It is doubtful that Swainson's Hawks can accomplish fattening of the magnitude necessary for this prolonged fast. Approximately half of the birds have little visible subcutaneous fat when they reach Panama, only about the halfway point of their journey. Although fasting migrants would incur a negative water balance and would need to drink periodically, observations of drinking during migration appear to be lacking. It seems improbable that a highly insectivorous raptor would reject food for a period of 5 weeks or more while traveling through regions which support some of the richest invertebrate faunas in the world; the adaptive value of such a behavior is not apparent.

¿Se abstienen de comer las rapaces migratorias de la especie *Buteo swainsoni* en su ruta a la Argentina?

EXTRACTO.—Algunos observadores sostienen que las aguilillas de la especie *Buteo swainsoni* no comen durante su migración desde Norte América a la Argentina, que puede durar 5 ó más semanas. Evidencias para tan prolongado ayuno son anecdóticas, especulativas y equívocas. Un ayuno migratorio de esta duración es fisiológica y ecológicamente improbable. Es dudoso que estas aves *Buteo swainsoni* puedan lograr un nutrimento de la necesaria magnitud para este prolongado ayuno. Aproximadamente la mitad de las aves tienen muy poca grasa subcutánea visible cuando ellas llegan a Panamá, que está aproximadamente en el punto medio de su travesía. Aun cuando los migrantes incurrieran en un balance negativo de agua y necesitaran beber periódicamente se observa que falta, al parecer, el hecho de beber durante la migración. Parece improbable que raptoras que son altamente insectívoras, omitan comer por un período de 5 ó más semanas, mientras viajan a través de regiones que ofrecen una de las más ricas faunas invertebradas del mundo. El valor que se adapte a tal conducta no es aparente.

[Traducción de Eudoxio Paredes-Ruiz]

The question of whether a particular avian species can meet its energy needs during long distance migration by relying on stored body fat, or by refueling (i.e., feeding) is intriguing. Remarkable examples of premigratory fattening and fasting migration have been documented in a number of avian species, which make long, nonstop flights over oceans, deserts or other inhospitable areas where refueling is difficult or impossible. Other migratory species migrate more slowly, alternating daily periods of movement with periodic rest stops. They typically feed *en route* as they encounter feeding opportunities.

Most migrant raptors use this "stop and go" migration pattern. Slower migrants may maintain somewhat elevated levels of stored body fat during migration, but this moderate fat depot appears to serve mainly as a reserve supply to carry them through periods of food scarcity. They do not store enough premigratory fat to fuel the entire migration. A re-

fueling strategy spares the use of this reserve supply of fat and may augment the fat depot when the migrant finds sufficient food supplies along the way (Berthold 1975).

Several workers have hypothesized that some neotropical raptors (e.g., Turkey Vultures *Cathartes aura*, Swainson's Hawks *Buteo swainsoni* and Broad-winged Hawks *Buteo platypterus*) fast during migration (Smith 1980, 1985, Smith et al. 1986, Houston 1987, 1990). These raptors often fly in large, concentrated flocks (kettles) between their north temperate breeding grounds and their non-breeding areas mainly in Central America or South America. The selective advantage of fasting migration (i.e., total abstention from feeding for prolonged periods) is not intuitively obvious. The stop and go pattern of migration should make refueling possible, unlike non-stop marathons where fasting is obligatory.

This commentary reexamines the evidence for

fasting migration in Swainson's Hawks. It critiques the energetic arguments previously used to support the hypothesis, considers the water budget constraints on migration, and examines the ecological plausibility of fasting migration in this species.

The Fasting Migration Hypothesis. Brown and Amadon (1968) reported the "general lore" that these species of raptors do not feed during migration. Smith (1980) presented the following evidence to support the fasting hypothesis: 1) the scarcity of published accounts of migrants seen feeding, 2) the reports from country people in Panama of both Swainson's and Broad-winged Hawks in weak condition on the ground below roosts and similar reports of exhausted Swainson's Hawks in Argentina, and 3) the absence of feces and pellets below roosts where thousands of the hawks had roosted the previous evening. Smith (1980) states that "most of the evidence is circumstantial, but, in total, supports the fasting hypothesis." Smith has argued that the massed flights and huge communal roosts would likely preclude most individuals from obtaining significant amounts of food under such crowded conditions, and that it would be more costly to forage and feed than to fast.

Smith (1985) elaborated on the scenario of an "anorexic migration strategy" by speculating that Swainson's Hawks feed copiously while wandering south in small groups, then cease feeding at about 30°N latitude when they begin massed flights. Smith (1985) estimated that the fasting migration lasted 50–60 d, based on the dates of passage of the first observed massed flocks at Las Cruces, New Mexico and Panama City and the time of arrival of Swainson's Hawks in Argentina. The duration of fasting migration was later revised downward to 37.5 d by assuming that a hawk averages 240 km/day throughout the 9000 km journey (Smith et al. 1986). A key assumption in their fasting migration hypothesis is that thermal soaring is a highly efficient mode of travel with very low energetic costs, only twice the basal metabolic rate.

Weaknesses in the Fasting Migration Hypothesis. The circumstantial evidence for prolonged fasting can be refuted in several ways. Concentrations of hundreds of migrating Swainson's Hawks have been observed as far north as Saskatchewan (Houston 1987, 1990), Washington and Montana (Bent 1937). These locations are 1500–2000 km north of the presumed extent of massed migration and would apparently add at least another week of travel to the required duration of fasting, assuming the rationale

that massed flights preclude feeding. Smith (1985) acknowledged some published accounts of Swainson's Hawks feeding in large groups in Texas (Littlefield 1973) and in Costa Rica (Slud 1964). Large assemblages of Swainson's Hawks also have been seen feeding in Washington and California (Bent 1937), Idaho (Johnson et al. 1987), and near Veracruz, Mexico (M. Ramos, pers. comm.).

Although mass roosts of these migrant hawks in Panama are reported to lack feces, feces were present at mass roosting sites of migrant hawks in Arizona (Henshaw 1875 in Bent 1937) and in Mexico (M. Ramos, pers. comm.). It is possible that during the first hours of light each day, before thermal soaring is feasible, most hawks disperse from roosts, regurgitate pellets and then feed mainly on insects. Most of the resulting excrement from that early morning meal would be eliminated during the following 10-hour flight period. Rates of food passage through the gastrointestinal tracts of raptors have not been determined, but judging from the rates of food passage in other avian species, it is reasonable to assume that a Swainson's Hawk would eliminate the bulk of an early morning meal before arriving at the evening roost (G. Duke, pers. comm.). If hawks have virtually emptied their gastrointestinal tracts before they enter an evening roost, little fecal or pellet material should be found beneath an infrequently used roost.

Reports of southbound hawks arriving in a weakened condition in Panamanian roosts (Smith 1980) suggest that some hawks become undernourished when they reach maximally crowded conditions in the geographical bottleneck of the Central American isthmus. However, undernutrition could be due to poor foraging success, rather than absolute fasting. The presence of emaciated migrant Swainson's Hawks in Central America indicates that some hawks deplete their limited energy stores much earlier than should be the case according to the fasting migration hypothesis. Indeed, the observation of emaciated Swainson's Hawks in Panama supports the alternative hypothesis that migrant hawks typically carry only moderate fat reserves which may be seriously depleted if the birds fail to find sufficient nourishment along the way.

Problems with the Predicted Duration of Fasting. The speculation that hawks fast for 5–8 wk during migration is a major weakness of the fasting hypothesis. Could a hawk, even at rest, survive such a long period of food deprivation? Using Smith's

(1980) original estimates of migration duration (60 d) and Swainson's Hawk lean body mass (900–1000 g), approximately 420–450 g of stored fat would be required for standard metabolism (SMR) alone (Aschoff and Pohl 1970). This fat depot would constitute 45–47% of the original body mass. In this computation, the fat has not been included as metabolically active tissue.

The required amount of fat storage would have to be even larger than the above estimate, because a bird in migratory flight should require more energy than a bird at rest (e.g., $2 \times$ SMR; Baudinette and Schmidt-Nielsen 1974), and a soaring bird carrying such a heavy burden of body fat should expend more energy per distance traveled than a bird at its optimal flight mass.

Smith's (1980) original estimate of Swainson's Hawk body masses (900–1000 g) is similar to the body masses determined by Craighead and Craighead (1956) ($\delta = 908$ g; $\text{♀} = 1069$ g), Fitzner (1978) ($\delta = 747$ g; $\text{♀} = 1080$ g), and Smith et al. (1986) ($\delta = 723$ g; $\text{♀} = 966$ g). These data indicate that females average about 160–260 g heavier than males. In later publications Smith (1985) and Smith et al. (1986) arbitrarily select a lean body mass of 600 g for male Swainson's Hawks, a seemingly low estimate, to compute the energy cost of migration. They did not attempt to model the energetics of females which reportedly weigh 900–1000 g.

Smith (1985) stated that if the lean body mass of a Swainson's Hawk is 600 g and its fat mass is 240 g "it could easily make the flight between Argentina and southern North America in 60 days without feeding." Smith's estimate, which assumes the catabolism of 4 g of fat per d (or 159 kJ/d; assuming that fat averages 39.7 kJ/g), would only supply 77% of the energy required for standard metabolism of a non-passerine bird of that body mass (Aschoff and Pohl 1970), or 88% of the estimated resting metabolism of a diurnal raptor of that size (Wasser 1986). Smith's (1985) metabolic estimate is far below that which would reasonably be expected for a bird in active migration.

Using a computer modeling technique, Smith et al. (1986) offered a revised estimate indicating that a male Swainson's Hawk (lean body mass = 600 g) would catabolize approximately 8.8 g of fat per day or 330 g of fat for a 9000 km flight. In the model, they assumed that the energy cost of flight is only twice the basal metabolic rate, roosting metabolism is 80% of standard metabolism, and migration speed averages 240 km/d (a 37.5 d journey). Furthermore,

they contended that the storage of such a large fat depot (55% of the lean mass) is "physiologically reasonable" (Smith et al. 1986).

Problems with the Necessary Amount of Stored Fat. The implausibility of a large raptor storing enough fat to sustain a fasting migratory journey lasting many weeks is another major weakness of the fasting migration hypothesis. It is doubtful whether Swainson's Hawks can accomplish fattening of the magnitude necessary for this prolonged fast. An exhaustive study of the body composition of 688 migrant Goshawks (*Accipiter gentilis*) in Sweden showed maximum fat levels of 14.1% and 17.2% of body mass in males and females, respectively (Marcstrom and Kenward 1980). Gessaman (1979) reported premigratory fat levels in American Kestrels (*Falco sparverius*) averaging 5–7% of the total body mass.

Little is known about the size of fat deposits of most diurnal raptors, but workers have frequently assumed that substantial differences in the average body masses of adults at different times of the year represent changes mainly in the amount of stored fat. The greatest body mass fluctuations in adult raptors have been recorded as the measured differences in body mass of females in egg laying condition versus non-breeding condition. Newton (1979) described the "great increase" in the mass of female European Sparrowhawks (*Accipiter nisus*) from a prelaying average of 300 g to an average at the peak of laying of 345 g, an increase of 15%. Similarly, female American Kestrels average approximately 29% heavier during the laying period in May than during July, the month of their lowest average mass of 109 g (J.S. Kirkley, unpubl. data). Extreme levels of premigratory fattening (30–47%) have been found only among small birds which make long, nonstop flights; the average fat reserves of even the larger limicoline birds (i.e., sandpipers and plovers) do not exceed more than 20% of the live mass (Berthold 1975).

The limited information on raptor body mass fluctuations does not support the contention that male Swainson's Hawks can store fat equal to 55% of their lean mass or 35% of their total body mass. Female Swainson's Hawks would require proportionately similar increases in their body masses, because their 160–260 g larger body masses should, according to allometric predictions, require the catabolism of at least 17–23% more fat than is needed for males. Smith et al. (1986) assumed that the additional energetic costs of carrying these large bur-

dens of body fat would be taken into account by using total body mass rather than lean mass in the allometric equations for estimating energy expenditures. Whether this allowance actually overestimates the true rate of energy expenditure, as Smith et al. (1986) contend, remains an unanswered question.

Quantitative measurements of stored fat in Swainson's Hawks are lacking. Smith et al. (1986) estimated the relative fatness of southbound hawks captured from mass roosts in Panama by inspecting their visible subcutaneous fat. The investigators judged only 8% (5 of 64) of the Swainson's Hawks to be very fat (fat index = 3), whereas 41% of the juveniles and 51% of the adults had little or no visible fat (fat index = 1 or 0). Low subcutaneous fat indices in a migrant should indicate that body fat is nearly depleted, because subcutaneous fat is considered to be the last region of body fat to be utilized (Blem 1989).

These fat index data pose a serious objection to the fasting migration scenario. Nearly half of the hawks examined had practically exhausted their fuel supply at slightly less than the halfway point of their hypothetical 9000 km fasting journey. Swainson's Hawks, at that point, should be carrying more than half of the original fat depot (at least 165 g of fat in males, or 28% of their lean body mass). A hawk (600 g lean mass) possessing over 165 g of fat should certainly have sufficient subcutaneous fat to be visually judged "very fat." In contrast, only 8% of the Swainson's Hawks were judged to be "very fat." These data alone refute the idea that most Swainson's Hawks fast for the entire duration of migration.

Water Budget Considerations. The respiratory water losses of fasting migratory birds should exceed their rates of metabolic water production; this negative water balance will be even more severe if substantial cutaneous water losses occur (Hart and Berger 1972). An estimated rate of fat oxidation of 8.8 g/d (Smith et al. 1986) would yield 9.4 g of water, assuming oxidation of one gram of fat yields 1.071 g of water (Schmidt-Nielsen 1964:30). The estimated minimum rate of evaporative water loss of a resting 600 g hawk would be approximately 18.3 g/d (Crawford and Lasiewski 1968, equation 6). The calculated minimum water deficit would, therefore, be approximately 9 g/d (1.5% of lean body mass). This value probably underestimates the daily water deficit of a fasting hawk, because rates of evaporative water loss should increase with the higher rates of pulmonary ventilation expected to accompany elevated metabolism during flight. Higher rates

of cutaneous evaporation should also result from increased convection during flight. The magnitude of the water budget deficit would increase even further if there were any excretory water losses or if fasting hawks ever had to pant to cool themselves in the high temperatures and intense sunlight of those subtropical and equatorial regions.

Basal rates of evaporative water loss would, alone, amount to more than 10% of a fasting hawk's lean body mass per week. With the likely routes of additional water loss, a fasting migrant hawk probably would need to drink, each week, a quantity of water equal to 15–20% of its lean body mass to offset its water deficit. Normally, raptors do not drink water, because they obtain sufficient water from the prey they consume (Bartholomew and Cade 1963). If the fasting migration hypothesis were valid, massed flocks of fasting hawks should be seen occasionally drinking at open water (undoubtedly a memorable spectacle), yet I have not read or heard of such behavior. Lack of evidence of drinking lends support to the contention that migrating hawks must be maintaining their water balance by feeding *en route*.

Ecological Considerations. A final argument against the fasting migration hypothesis is the one that seems most obvious from an ecological standpoint. Prolonged fasting migration is only typical of birds which fly nonstop over inhospitable barriers such as deserts or bodies of water. What is the ecological barrier posed by the migration route of Swainson's Hawks? Apparently none. Like many species of gulls, Swainson's Hawks are known to congregate on the ground in large flocks and to gorge themselves on grasshoppers, crickets and other insects (Bent 1937, Johnson et al. 1987). Are the flocks of Swainson's Hawks always so large as to preclude them from exploiting insects they encounter throughout the 9000 km journey? It is difficult to imagine that Swainson's Hawks would terminate all feeding during those many weeks of travel through the tropics and subtropics, particularly since those areas are rich in insect abundance. In conclusion, there appears to be no obvious ecological necessity for prolonged fasting by any of the raptors migrating through the Neotropics.

Insects should be especially abundant during the southward passage of hawks in October, because this is the tropical rainy season with its accompanying resurgence of vegetation and insect life. Rainstorms lasting several days are not uncommon in the subtropics of Mexico and Central America, and these storms are known to effectively ground Swainson's

and Broad-winged Hawks (M. Ramos, pers. comm.). When thermal soaring migration of these hawks is delayed, as it is on rainy days and during the first hours of light each morning, the hawks should be expected to disperse from their roosts and hunt for food.

Speculations which attempt to extrapolate the behavior of southbound Swainson's Hawks in Panama to their entire 9000 km journey may lead to erroneous conclusions. Questionable energetic parameters may add overly optimistic support for the plausibility of fasting migration. Further studies are needed which actually document the behavior of members of individual flocks for several consecutive weeks. These studies should include continuous monitoring of massed flocks as they move through Mexico, Central America and South America. Predicted behavior, based on the considerations presented in this commentary, would include opportunistic feeding by hawks when they are not involved in thermal soaring, and no drinking. Periods of fasting or undernourishment, should be short-term, and feeding should commence when insect infestations and other prey are opportunistically encountered.

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